It is not such an energetic bird as others of the family, and does not remain on the wing for so long a time, preferring to rest for considerable periods on dead trees, of which it nearly always selects the largest. These Swallows sit in small parties of five to eight on a tree singing away gaily, whilst others preen themselves. Every now and again they all leave together, take a short flight, and again return one by one.

VIII.—*On the Anatomy of the Kingfishers, with Special Reference to the Conditions in the Wing known as Eutaxy and Diastataxy.* By P. Chalmers Mitchell, F.Z.S., F.L.S.

(Plates IV. & V.)

Since the classical observations of Wray (1) were published, it has been known that in many birds a gap occurs in the series of cubital quills after the fourth large quill, while in other birds no such gap is found. The term *aquintocubital* was applied to the former condition, and *quintocubital* to the latter, as it seemed that in the one the fifth cubital quill, counting upwards from the wrist, was missing, while in the other it was present. In 1899 Mr. Pycraft and I made simultaneous communications (7 and 8) to the Linnean Society, in which we brought forward reasons against the supposition that the aquintocubital condition was due to the loss of a quill, and we adopted my name *diastataxy* to indicate the condition in which there was a diastema or gap in the series, *eutaxy* for the condition devoid of a gap. In the communication referred to, I showed that among the Columbidæ both eutaxy and diastataxy occurred, and gave a series of anatomical facts which seemed to bear the interpretation that those birds presenting the eutaxic condition were more modified than those with the gap in the quill series. It has been known for some time that the two conditions were both present among the Kingfishers. I have had the opportunity in the Prosectorium of the Zoological Society of

examining a number of Kingfishers; my thanks for materials are due to the Society, to the Prosector, Mr. Beddard, and to Mr. C. Hose of Borneo. I hope to show that in the Alcedinidæ, as in the Columbidæ, those forms which have the eutaxic arrangement of the wing are in other respects more modified. The species which I have had an opportunity of examining are:—

Dacelo gigantea.
Sauropatis chloris.
—— sancta.
—— sordida.
—— vagans.
Ceryle maxima.
—— alcyon.
Halcyon pileata.
—— rufa (coromanda *Sharpe*) (Callalcyon rufa).
Ceryle americana.
—— inda.
Cittura cyanotis.
—— sanghirensis.
Alcedo asiatica.
—— bengalensis.
—— ispida.
Ceyx rufidorsa.

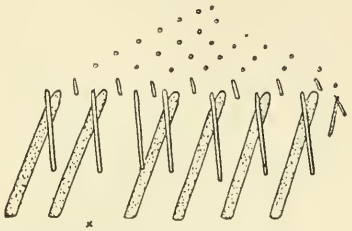
The identification of some of these was simple; in other cases I am indebted to the kind assistance of Dr. Bowdler Sharpe; the species of *Cittura* were identified at the Zoological Gardens by Mr. Forbes, Mr. Beddard's well-known predecessor. There is difference of opinion as to the allocation of the generic names *Sauropatis* and *Halcyon*; I agree with Beddard (4) that, so far as we have examined the species, there are anatomical reasons for separating the genera, and I follow him in using the name *Halcyon* for the red-billed species. This, however, affects the nomenclature and not the conclusions, as the species were readily distinguishable.

Eutaxy and Diastataxy.

It is easy to make out that in most Kingfishers the wing-feathers are arranged in rows more or less diagonally placed; the large quill is at the base of the row and there follow above it the major covert and the coverts of the third and fourth series. Owing to the great size of the quills and relative size of the major coverts the rows are dislocated at the end towards the ulna; they are shorter at the wrist, and increase in length as the surface of the wing widens out

towards the elbow. In *Dacelo gigantea* (fig. 4) there is a small carpal remex and covert, represented to the right, and attached by a small fold of membrane to the first large cubital quill in the fashion which I described in the Pigeons (7). Then follow four ordinary quills; then the diastema, and thereafter

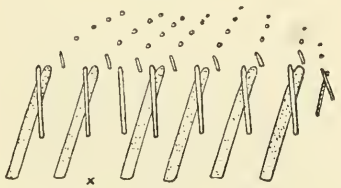
Fig. 4.



Dacelo gigantea, diagram of cubital feathering, the wrist being to the right, the elbow to the left. The quills are large, and dotted in the figure; the major coverts cross them; the feathers of the diagonal rows are represented as small circles. To the right is the small carpal remex and carpal covert. × diastataxic gap.

quills in even series. Each quill is at the base of a diagonal row, the major covert forming the feather in the row nearest the quill. In the diastataxic group there is a similar row, rather shorter, however, than the other rows. The four species of *Sauropatis* (fig. 5) present a condition essentially

Fig. 5.

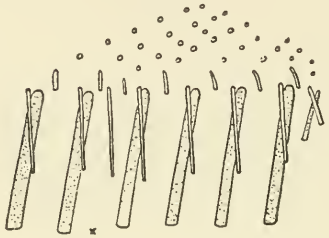


Sauropatis, diagram of cubital feathering. Explanation as in figure 4.

similar. The diagonal row in the diastataxic gap is relatively rather longer. In *Ceryle maxima* (fig. 6, p. 100) and *Ceryle alcyon* there is a carpal covert and carpal remex as before. There is a gap in the usual diastataxic position, and this, although relatively smaller than in *Dacelo* and *Sauropatis*, is

occupied by a diagonal row. The seven species of Kingfishers mentioned in the first column of the list given above are diastataxic; in five of them the gap is almost as wide as the space for a complete row with a quill; in two, the gap

Fig. 6.

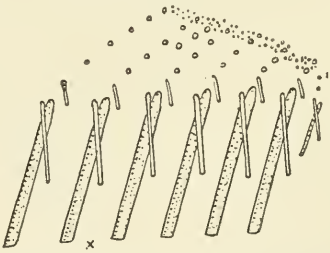


Ceryle maxima, diagram of cubital feathering. Explanation as in figure 4. The diastataxic gap (×) is small, but is occupied by a diagonal row, complete save for a quill.

is narrower, but in all it is occupied by a fairly complete row of feathers.

Halcyon pileata (fig. 7) must certainly be described as eutaxic. The carpal covert and carpal remex are normal, the latter bound down by the usual plica. Then follow the

Fig. 7.

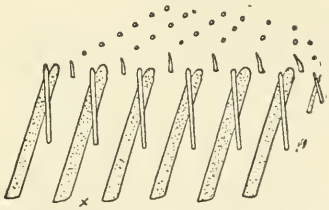


Halcyon pileata, diagram of cubital feathering. Explanation as in figure 4. Eutaxic arrangement, but position of diastataxic gap (×) marked by vestige of a diagonal row, consisting of three feathers.

secondary quills in even series, each at the base of a diagonal row. But in the position of the diastataxic gap, although there is no gap, and no trace of the so-called major covert that occupies the base of the row in diastataxic birds, there

is a trace of the diastataxic row in the form of three feathers occupying the upper part of what probably has been a row. I may mention here that in one of the eutaxic Cuckoos (*Carpococcyx radiatus*) I have found a similar vestige of what I regard as the old diastataxic condition. *Halcyon rufa* (fig. 8) is also eutaxic, but in it there is no vestige of the

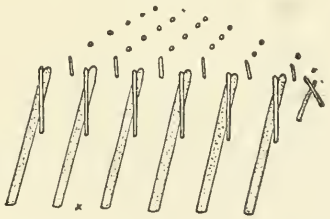
Fig. 8.



Halcyon rufa, diagram of cubital feathering. Complete eutaxic arrangement, there being no gap nor remnant of a row in the diastataxic position.

other condition. The carpal remex is extremely small, smaller relatively than it is represented in the diagram, and it is not bound to the adjacent cubital by the usual plica. The covert is normal, and then follow the cubitals with their diagonal rows in even series. Although *Ceryle maxima* and *C. alcyon* are diastataxic, *C. americana* and *C. inda* (fig. 9)

Fig. 9.

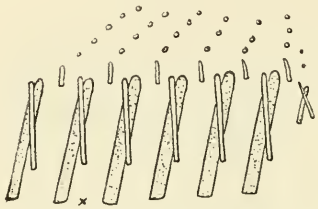


Ceryle inda and *C. americana*, diagram of cubital feathering. Explanation as in figure 8. Eutaxic arrangement.

are eutaxic. In these, which are practically identical in this respect, the carpal remex is tied to the first quill by the usual plica; the covert is small. The quills follow in even

series each with its diagonal row. *Cittura cyanotis* (fig. 10) and *C. sanghirensis* are also eutaxic in the strictest sense. In these, there is a small carpal remex not bound down by a plica, and a very small carpal covert. Then follow thirteen quills in even series, each supporting a diagonal row.

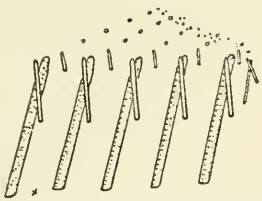
Fig. 10.



Cittura cyanotis, diagram of cubital feathering. Explanation as in figure 8. Eutaxic arrangement.

Alcedo asiatica (fig. 11), *A. bengalensis*, and *A. ispida* are all strictly eutaxic; the carpal covert and carpal remex are absent in *A. ispida* and present in the others. In all of them the quills are in even series, and are at the base of diagonal rows. The wing of *Ceyx rufidorsa* is similar to that of *A. asiatica*.

Fig. 11.



Alcedo asiatica, diagram of cubital feathering. Explanation as in figure 8. Eutaxic arrangement.

The seventeen Kingfishers which I have examined thus show plainly that here, as in the Columbidæ, the conditions known as eutaxy and diastataxy cannot be regarded as fundamental characters in any of the greater schemes of classification. Both conditions occur, scattered as it were indiscriminately within the confines of the group, and sometimes even within the confines of a genus. Nor are the two conditions absolutely marked off one from another, but lend

themselves to an arrangement in a graded series, which suggests the production of one condition as a simple modification of the other. At one end of such a series stand *Dacelo* and *Sauropatis*, diastataxic in the strictest sense, there being a wide gap in the quill series, and this gap, with the exception of the quill, being occupied by a complete diagonal row. Next come *Ceryle maxima* and *C. alcyon*, still diastataxic but with the width of the gap much reduced. Then comes *Halcyon pileata*, eutaxic, without a gap, but with a possible remnant of the other condition in the form of a reduced diagonal row of three small feathers. Then come the other eutaxic forms with no gap and no trace of the diastataxic diagonal row. In my paper on the wings of the Columbidæ I advanced an hypothesis that the diastataxic condition was primitive, and suggested a mode in which it might have arisen. Without for the present recurring to that suggested origin, I am content to point out that were the wings of all birds originally diastataxic it is not difficult to see that by closing of the gap, and consequent gradual obliteration of the row that occupied the gap, the eutaxic condition might have been produced. Moreover, if the production of eutaxy be part of a general process of the formation of a simpler but more specialized organ of flight from an older and more diffusely arranged organ, there is no theoretical difficulty in supposing it to have been produced separately and independently in many different kinds of birds. On the other hand, if so remarkable an arrangement as the absence of a single quill, in a definite and identical position, has been produced from a primitive eutaxy, we have either to make the supposition that all the diastataxic forms are more closely related to each other than to the eutaxic forms—a suggestion that strikes rudely across all natural classifications—or to face the almost impossible idea of its polyphyletic origin. I will now proceed to review the anatomical facts which serve to show that the eutaxic Kingfishers are in other respects the more specialized birds.

There is not much information to be derived from the geographical distribution and external characters of the

seventeen forms under notice. Austro-Malaya is the metropolis of the Kingfishers, and contains both eutaxic and diastataxic forms. Such presumably far-travelled forms as the American *H. rufa* and *C. americana* are eutaxic, as is also the European *Alcedo*. The presence of a tuft on the oil-gland is almost certainly the more primitive condition among Kingfishers. The *Cittura*, in which the gland is naked, are eutaxic. Forbes mentions that the gland is also naked in *Tanysiptera*; it would be interesting to find if that genus also is eutaxic. The characteristic arrangement of the ventral pterylæ in the Kingfishers is that the ventral tract, as in *Alcedo*, divides at the base of the neck into two lateral tracts, each of which almost immediately divides again. This arrangement is well marked in all the eutaxic forms, in *Dacelo*, and in *Ceryle maxima*. In one of the eutaxic forms, *Ceryle americana*, the median divisions of the lateral tracts coalesce soon after their separation from the lateral divisions, and then separate again. A similar condition is seen in the diastataxic *C. alcyon*. But in the species of *Sauropatis*, although least so in *S. sancta*, there is a broad, diffuse, pectoral tract, hardly distinguishable into lateral tracts. I do not quite agree with Beddard, who called attention to this, that it can be regarded as a generic character of *Sauropatis*, as it is not so apparent in *Sauropatis sancta*; but it is interesting to notice that the forms in which this absence of differentiation occurs are diastataxic. The wings of the eutaxic forms have on the whole a smaller number of secondary quills, and these individually are larger; the carpal covert and carpal remex tend to be smaller, and are absent in one of the *Alcedines*. The eutaxic *Ceyx* has the second toe absent, certainly not a primitive character.

Muscular Anatomy.

Biventer Link.—The only noteworthy peculiarity that I have found in the muscles of the head and neck relates to a tendinous link first noted by Dr. R. O. Cunningham (3) as uniting the *biventres cervicis muscles* in *Ceryle stellata*, but absent in *Alcedo*. Beddard (4) examined a number of

Kingfishers with reference to this point, and I paid minute attention to it as a character known to differ among Kingfishers. It is probable that its presence is a Kingfisher character; so far as I know, it is not found in other birds, and it seems too definite to have been acquired independently in a number of cases. Its absence seems best explained as a secondary loss. Beddard noticed that it was present in one of two specimens of *Sauropatis vagans*; I found it absent in one *S. vagans* and in *S. chloris*, but an apparently degenerate slip represented it in *S. sancta* and *S. sordida*. It is absent in *Alcedo ispida*, but a diagonal slip represents it in *Alcedo asiatica* and *A. bengalensis*. Assuming, then, that the loss is secondary, it appears that the eutaxic forms *Ceyx*, *Halcyon rufa*, and *H. pileata* have lost it; one of the *Alcedines* has lost it, and in the others it is degenerate. In *Sauropatis* it is present, absent, or degenerate; in *Dacelo* it is absent, in the other forms, eutaxic or diastataxic, it is present. Here, as in many other characters, there is not a definite coincidence between eutaxy and progressive change, but the more general fact holds good that, where there is a tendency within the group for independent movement in any direction, the eutaxic forms show a high relative average of instances of such change.

Latissimus dorsi, anterior et *posterior*.—The phylogeny of these muscles outside the Avian group is an extremely difficult problem, but I am on clear ground in stating that the most common and generalized condition among birds is the existence of an anterior and posterior division, the two being fairly equal in width and strength, well separated at their origins, and in contact at their insertions. Such a condition is well marked in all the diastataxic forms, although there is a tendency, displayed in *Dacelo* and in *Sauropatis*, for the anterior division to be weaker than the posterior. I follow Fürbringer in regarding any well-marked divergence from the condition described as secondary. Among the Columbidæ I found the divergent tendency to be in the direction of reduction of the posterior division, and this was well-marked among the eutaxic forms. In the Kingfishers

it is the anterior division that tends to be reduced; and this reduction, incipient in some of the diastataxic forms, becomes striking in eutaxic forms. Thus in the eutaxic *Ceryle americana* and *C. inda*, as compared with the diastataxic *C. maxima* and *C. alcyon*, the anterior division is very thin and weak; the posterior is enormous, broad, and strong, and with a considerable forward extension of its origin. In *Halcyon* a similar condition exists, less marked in *H. rufa*, plain in *H. pileata*. In *Cittura* it is plain; in *Alcedo ispida* the anterior division appears only as a few fibres; in *A. bengalensis*, *A. asiatica*, and in *Ceyx* the anterior division is absent, while the posterior has become very strong.

Latissimus dorsi metapatagialis.—This slip was equally developed in all.

Rhomboideus superficialis and *R. profundus*.—In the Kingfishers the superficial muscle extends further forwards, the deep muscle further postaxially, the two partially overlapping in the middle. These characteristics are accentuated in all the eutaxic forms. The deep muscle tends to be thicker at its anterior and posterior margins. This progress towards secondary cleavage is well advanced in *Sauropatis vagans*, alone in this respect among the diastataxic forms, while in the eutaxic *H. rufa*, the *Citturæ*, *Ceryle americana*, *Ceyx*, and the *Alcedines* it is obvious.

Supracoracoideus.—Markedly bipinnate in all and without notable variations.

Coraco-brachialis externus is in all a small fleshy muscle.

Coraco-brachialis internus is in all a small muscle arising from the postero-lateral part of the coracoid, with a slight overlap on to the sternum, and is inserted to the dorsal surface of the median tubercle of the humerus.

Biceps presents no marked differences, and the *biceps patagialis* is absent in all, as in the Passerines and other birds called *anomalogonatous* by Garrod.

Alar Muscles.—The wing is the most distinctive part of the Avian body, and the modifications in it deserve special attention when the relative specialization of different birds is being considered. The group of alar muscles and tendons

present an interesting series of modifications in Kingfishers, and in these the scale of specialization dips markedly towards the eutaxic forms.

Deltoides major.—There can be no doubt but that among birds generally this muscle tends to increase in length, its insertion extending gradually down the humerus. In *Dacelo* it has reached halfway down the humerus, and in the other diastataxic forms it has a nearly similar extension, sometimes falling short and sometimes just surpassing that length. In all the eutaxic forms it reaches down beyond the first half, although this downward extension always falls short of that attained in most Pigeons.

Deltoides minor.—This is in two portions, separated by the tendon of the *supracoracoideus*, and does not show any striking divergences in the different forms.

Deltoides propatagialis.—Many writers have made contributions to our knowledge of this distinctively Avian muscle, and Fürbringer in particular has classified the series of modifications which it presents. At one end of the series is the condition in which the muscle has a single belly, giving off at the distal end the *longus* and *brevis* tendons. This condition, obviously more primitive, occurs in most Avian families, and in all but a few exceptional cases among swimming and wading birds. In the next stage the distal extremity gives rise to two muscular peaks, one for the *brevis* and another, usually smaller, for the *longus* tendon. This condition occurs in a small number of genera scattered irregularly through the families. In further stages the peaks deepen, the division extending towards the origin of the muscle, such stages being of rarer occurrence. The culmination of the series has been attained in Passeres and in a few genera of other birds, in which the original muscle has been divided into a specialized and separate muscle for each tendon. In all the diastataxic Kingfishers the peaked stage has been reached. In *Dacelo* (Plate IV. fig. 1), in *Ceryle maxima* (Plate IV. fig. 2) and *C. alcyon* (Plate IV. fig. 3), and in all the species of *Sauropatis* (Plate IV. fig. 4) the *longus* peak is smaller than that for the *brevis*. Among

the eutaxic forms *C. americana* (Plate IV. fig. 5) alone has remained behindhand in the specialization of this muscle. In *C. inda* (Plate V. fig. 6), *H. pileata* (Plate V. fig. 8), *H. rufa* (Plate V. fig. 9), *Alcedo asiatica* (Plate V. fig. 10), *A. ispida*, *A. bengalensis*, and *Ceyx rufidorsa* the division is practically complete, so that the Passerine condition of two muscles has been reached. In *Cittura cyanotis* (Plate V. fig. 7) the same stage has been reached with the further specialization of the *brevis* division of the muscle into two minor peaks.

Pectoralis propatagialis.—The most common and widespread condition of the pectoral contribution to the alar muscles is the occurrence of a slip, muscular and tendinous, from the pectoral muscle to the *longus* and *brevis* tendons. This condition occurs in all the diastataxic forms (Plates IV. & V., various figures, *p.l.* and *p.b.*): in some of the eutaxic forms the *longus* division becomes more specialized; the *brevis* tends to disappear, in *Alcedo*, *Ceryle inda*, and *Ceyx rufidorsa* it has completely disappeared.

Alar Tendons.—The *deltoides propatagialis* and *pectorales propatagialis* are attached to a set of tendons of which the structure and modifications in birds generally have been attended to by Garrod, Gadow (9), Beddard, Fürbringer, and a host of other anatomists, Fürbringer in particular having made a great stride towards classification and coordination of the materials. In the *longus* tendon among Kingfishers I have not found differences of moment, but the *brevis* tendon offers conditions of great interest. I will begin by setting out the anatomical data. In *Ceryle maxima* (Plate IV. fig. 2) there is a broad diffuse band of fasciæ stretching from the *deltoides* to the extensor muscles, and receiving the *pectoralis* tendon. The edges of this are thickened, and a stronger slip, the "α" of Fürbringer, is attached to the *extensor metacarpi radialis*, distad of the main fasciæ. In *Ceryle alcyon* (Plate IV. fig. 3; and Beddard (4), fig. 2) there is a similar broad band of fasciæ, but in it three thicker strands exist. The first is in continuity with the peak of the patagial muscle most near the humerus, and at its distal end bends towards the elbow; it is the "γ" of

Fürbringer. The second is on the distal edge, arising chiefly from the *deltoides*, but partly from the *pectoralis*; it is the "α" of Fürbringer, and, as in *C. maxima*, is inserted to the *extensor metacarpi*, distad of the main tendinous mass. The third, the "β" of Fürbringer, is median, and arises chiefly in the line of the *pectoralis* contributor to the system. In *Sauropatis chloris* (Plate IV. fig. 4) and the other species I dissected (*S. albicilla* as shown by Beddard (4), fig. 3, very closely resembles the others) the fasciæ are much reduced, while the thickenings assume independent identity as tendons. The tendon on the humeral side obviously is homologous with the corresponding thickening in *Ceryle alcyon*, and is the "γ" of Fürbringer. The pectoralis contribution and the distal thickening unite, and then diverge distally into two branches—one, the "β" of Fürbringer, bending towards the humeral edge, joining with the tendon of insertion of "γ," and forming a fan-shaped extension over towards the ulnar edge of the forearm; the other turning wristwards is the "α" of Fürbringer. In *Dacelo* (Plate IV. fig. 1) there is a still smaller extent of undifferentiated fasciæ, and the appearance is that of two parallel tendons joined by a sloping band: the figure makes the homologies of these obvious; the parallel tendons are α and γ, with β running down from α to γ. In *Cittura* both species are alike in this matter (Plate V. fig. 7); the tendons are distinct and are not united by fasciæ, their condition obviously being a simple modification of that found in *Sauropatis*—α, β, γ being distinct distally, but β and α joining more proximally after origin from the *pectoralis* and distal peak of the *deltoides patagialis*. In *Halcyon rufa* (Plate V. fig. 9) α, β, and γ are distinguishable distally; in Beddard's figure (4, fig. 1) α is more separated from the common mass distally, and is therefore more like the condition in *H. pileata* (Plate V. fig. 8); but higher up all three blend into a single round tendon. In *Ceryle americana* (Plate IV. fig. 5) and in *Alcedo* (Plate V. fig. 10) α, β, and γ are distinct at their insertions, but, proximally, arise from a single well-rounded tendon. In *Ceryle inda* (Plate V. fig. 6)—and *Ceyx rufidorsa* closely

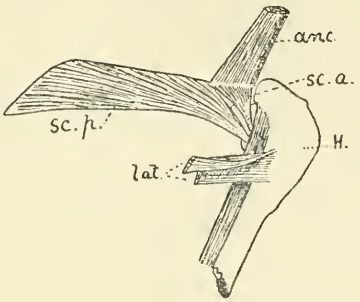
resembles this—the concentration is carried slightly further, β and γ alone being distinct at their insertions, while above there is a single round tendon.

The forms showing these conditions may obviously be placed in a series—the diastataxic forms led by *Ceryle maxima* being at one end, the eutaxic forms culminating in *Ceyx* and *Ceryle inda* being at the other. Beddard (4) has rightly remarked that the *Alcedo* type was anatomically the simplest of those with which he dealt, and obviously the *C. inda* type is still simpler. But it is no necessary conclusion that in an anatomical series the simpler structure is the more primitive. In the case of the alar tendons, Fürbringer has shown that the *brevis* tendons are to be regarded not as extensions of their muscles, but as differentiations of the originally diffuse alar fasciæ into which these muscles were inserted, the muscles themselves being originally cutaneous slips. From this point of view it is plain that the diffuse undifferentiated condition of *C. maxima* is the most primitive of the series; *C. alcyon* shows a differentiation of this diffuse structure by the appearance of thickenings, presumably along the lines of strain; *Sauropatis, Halcyon,* and *Cittura* show, so to speak, a cutting away of the unnecessary diffuse fasciæ between the thickenings, with the result that the latter appear as independent tendons. In the other eutaxic forms these tendons become simplified by concrescence until the Passerine single-tendon condition is reached; but the distal ends may still retain traces of the differentiation into α, β, and γ. Thus it would appear that in this case, as in the case of the splitting of the *deltoides patagialis,* the eutaxic forms display the higher stages of progressive specialization. Curiously enough, in this case, as in that of some structures among Pigeons, the degree of differentiation reached by eutaxic forms shows interesting resemblances to well-known features of the Passerine structure.

Scapulo-humerales anterior et *posterior.*—The condition of these muscles in the Kingfishers is that found in most groups of birds. As in *Dacelo* (fig. 12), both muscles are present; they meet at their origin from the scapula, but remain quite

distinct to their insertions. The posterior muscle is very much larger than the anterior. As exceptions, I found in the eutaxic *Alcedines* and in *Cittura sanghirensis* that the anterior muscle was relatively smaller.

Fig. 12.



Humeral muscles of *Dacelo gigantea*.

H., humerus; *anc.*, anconæus scapularis, cut short; *sc.a.*, scapuli-humeralis anterior; *sc.p.*, scapuli-humeralis posterior; *lat.*, latissimus dorsi, anterior et posterior.

Subcoraco-scapularis.—In all the Kingfishers the *subscapularis* portion of this compound muscle is in two divisions, separated by the insertion of the *serratus* slip. In *Dacelo* the *externus* is much larger than the *internus*, and its insertion reaches nearly opposite the point where the scapula bends downwards. The origin of the *internus* just reaches the clavicle. In *Ceryle maxima* the clavicular origin is more marked, and the same condition is present in the other forms. The coracoid division of the muscle is large and normal in all the *Cerylæ*, in the species of *Sauropatis*, in the *Alcedines*, in *Ceyx*, and in *Halcyon rufa*, extending down to the *sterno-coracoid*; but in *Halcyon pileata* and in *Dacelo* it is reduced to a slender ligament. These may be individual variations, but they are interesting as suggesting a tendency to change in this generally constant muscle.

Anconæus and *Expansor secundariorum.*—The scapular and humeral portions of the muscle are well developed, and practically identical in all the Kingfishers, but that specialized portion of the muscle called the *expansor secundariorum* by

Garrod offers important differences. It is present but feeble in *Dacelo*, *Ceryle maxima* and *C. alcyon*, and in the species of *Sauropatis*—that is to say, in all the diastataxic forms. It is also present in *Halcyon rufa*, a eutaxic form, but is absent in *H. pileata*, *Ceryle inda* and *C. americana*, the two species of *Cittura*, the *Alcedines*, and *Ceyx rufidorsa*—that is to say, in all but one of the eutaxic forms, an obviously secondary condition.

Musculature of Forearm and Hand.—In this series of muscles the only case of striking difference occurs in the *extensor indicis longus*. In *Dacelo* this arises from the middle half of the radius on its ulnar face, and is inserted to the phalanges of the second digit. The short head from the distal end of the radius, present in some birds, is absent. In all the diastataxic forms the muscle is like that in *Dacelo*; in all the eutaxic forms its origin has a longer extension, occupying about the middle two-thirds of the radius, and otherwise is relatively stronger.

Musculature of the Thigh and Leg.—Kingfishers are birds in which flight is the most important mode of progression, and in which the hind limbs play a relatively smaller part in the activities of life. Probably, in relation to this, the wings and shoulder-girdle tend to increase in relative size and strength, while the pelvis and legs tend to diminish in size. This double tendency is plain in all, but reaches a maximum in eutaxic forms, such as the species of *Alcedo* and *Ceyx*. The changes are plain both in the skeleton and in the soft parts.

Ilio-tibialis externus seu *sartorius*.—In *Dacelo* the origin is tendinous from the supra-iliac crest, with a forward extension to the second last dorsal vertebra. From this the muscle runs with a narrow belly to the tendinous insertion in the knee-capsule. The relations are similar in *Ceryle maxima*; in *C. alcyon* the belly is rather broader, while in the eutaxic *Cerylæ* the increase in breadth is enormous. The species of *Sauropatis* resemble *Dacelo* and the diastataxic *Ceryles*. In the *Halcyones*, *Cittura*, and *Ceyx* the belly is also narrow, but in the *Alcedines* it is very broad. There is

therefore evidence that in the Kingfishers this muscle tends to change from the more usual condition in birds, increasing in breadth and strength at the expense of the glutæus maximus. The contrast is most apparent when taken between the diastataxic and eutaxic *Ceryles*, but it also occurs between eutaxic *Alcedines* and the diastataxic forms.

Ilio-tibialis seu *glutæus maximus*.—The researches of Garrod would seem to imply that the generalized Avian condition of this muscle is broad and strong, its origin from the ilium or dorsal middle line extending behind and in front of the acetabulum. In *Dacelo* alone I have found a trace, in the form of fasciæ, of the postacetabular portion. In *Dacelo*, *Ceryle maxima*, *C. alcyon*, and the species of *Sauropatis*—that is to say, in all the diastataxic forms—the preacetabular portion of this muscle is well developed. Among the eutaxic forms *Cittura sanghirensis* alone has retained this condition; in *Cittura cyanotis*, *Halcyon rufa*, and *Ceyx rufidorsa* the muscular belly is very narrow and weak; in *Halcyon pileata*, *Ceryle americana* and *C. inda*, and in the *Alcedines* the reduction is carried so far that the muscle is represented by a band of fasciæ with only a few muscular fibres near the proximal end.

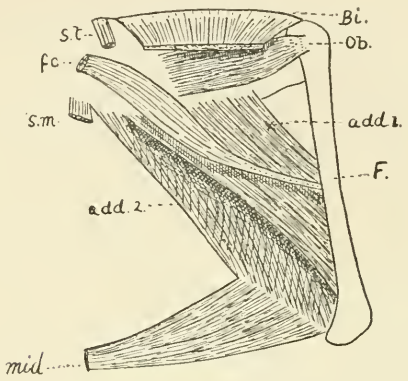
Ilio-trochanterici seu *glutæi*.—In *Dacelo* all three are distinct and separate: the *posterior* (*secundus*) is very large, and arises from all the preacetabular ilium; its insertion, partly fleshy, partly tendinous, is to the femur, proximad of the insertions of the others. The *anterior* (*tertius*) is the next in size and the most distal. The *medius* (*quartus*) is the smallest, and lies under the *posterior* and between it and the *anterior*. In all the other Kingfishers the condition of these muscles was similar except that in *Halcyon pileata* the *medius* was reduced to the merest vestige.

Ilio-femoralis externus (*glutæus anterior*) was absent in all.

Femori-tibiales (*cruræus* plus *vastus* and *vastus internus*).—The *internus* in all has the normal arrangement; the *vastus* and *cruræus* are also normal, but in the species of *Ceryle* there is also an insertion to the lower part of the femur, an arrangement not uncommon in birds.

Caud-ilio-femoralis.—The *pars iliaca* (*accessory femoro-caudal*) is absent in all. The *pars caudalis* is present in all,

Fig. 13.

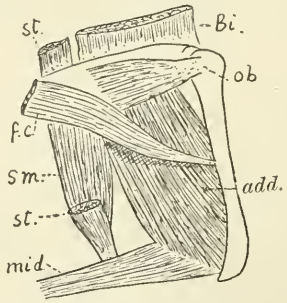


Femoral muscles of *Ceryle maxima*.

F., femur; *Bi.*, biceps cut short; *f.c.*, femoro-caudal; *s.t.*, semi-tendinosus, cut short; *s.m.*, semi-membranosus, cut short; *ob.*, obturator externus; *add.* 1, adductor externus; *add.* 2, adductor internus; *mid.*, middle head of the gastrocnemius.

and is comparatively narrow in *Dacelo*, in *Ceryle maxima* (fig. 13, *f.c.*) and *C. alcyon*, *Sauropatis vagans*, and *Ceyx rufidorsa*; while in *Ceryle inda* (fig. 14, *f.c.*), *C. americana*,

Fig. 14.



Femoral muscles of *Ceryle inda*. Lettering as in figure 13.

the *Cittura*, *Alcedines*, and in *Sauropatis sordida*, *chloris*, and *sancta* there is no well-marked relation between the

conditions of the muscle and the eutaxy or diastataxy, but, so far as it goes, the width is more often greater in the *eutaxic* forms. The instances in the figures do not show the contrast in its most marked state.

Caud-ilio-flexorius.—The *accessory semi-tendinosus* is possibly represented by a few fibres in *Dacelo*; it is absent in the others. The *semi-tendinosus* in all is inserted to the tendon of the *semi-membranosus*; it is rather wider in those forms in which the *femoro-caudal* is wide (figs. 13, 14, *s.t.*).

Ischio-flexorius (*semi-membranosus*) in all is larger than the *semi-tendinosus*, and is inserted to the tibia by a flat tendon (figs. 13, 14, *s.m.*; fig. 15, *semi-m.*). It also varies in width with the width of the *femoro-caudal*, the increased width being specially marked in the eutaxic *Ceryles*.

Biceps in all is a strong muscle with a very wide origin and the usual sling.

Ischio-femoralis (*obturator externus*) differs slightly but irregularly in the extent of its origin from the pelvis, being rather shorter in some of the eutaxic forms (figs. 13 and 14, *ob.*). But in these cases another feature, the shortening of the pelvis, must be kept in view, and it is by no means certain that there is a definite relation between the changes of size of the bone and the muscle. There is some evidence that the pelvis is becoming shorter in the more specialized Kingfishers, and unless the muscle is shortened at precisely the same rate, a shortened pelvis would conceal a simultaneous shortening of the muscle. This raises the very large and important question of the independence of the "growth forces," which in some cases seem to be displayed by different parts of an organism, while in other cases alteration in parts seems to be accompanied by a recovery of the original symmetry. I do not think that there is at present enough material for the discussion of this subject.

Pub-ischio-femorales (*adductors*).—*Ceryle maxima* (fig. 13, *add.* 1, *add.* 2) and *C. inda* (fig. 14, *add.*) show two conditions. In *C. maxima* the *superior adductor* is much smaller and distinct, having no connection with the *gastrocnemius*, while the *internus* is fused along a diagonal seam with the

middle head of the *gastrocnemius*. This condition is typical in Kingfishers and is common in birds. It occurs in *Dacelo*, *Ceryle maxima*, four species of *Sauropatis*, the *Halcyones*, *Cittura*, *Ceyx*, *Alcedo asiatica*, and *A. bengalensis*. On the other hand, in *Ceryle alcyon*, a diastataxic form, in *C. americana*, *C. inda* (fig. 14, *add.*), and *Alcedo ispida*, while the *internus* is similar, the *externus* is either so small as to be practically indistinguishable (*Alcedo*) or has lost separate identity.

Popliteus consists in all of a few fibres nearly transversely arranged between the heads of the tibia and fibula.

Tibialis anticus in all has the usual fleshy head from the tibial crest and tendinous head from the external condyle of the femur. It passes under a fibrous transverse bridge, and is inserted by a single tendon.

Extensor digitorum communis in *Dacelo* arises in the normal fashion under the *tibialis anticus*; it is inserted to the three digits by three distinct slips. In all the Kingfishers it is similar, except that in *Ceyx* the slip to the index is absent.

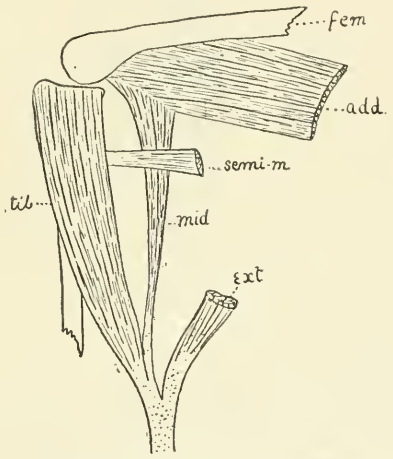
Peroneus superficialis.—This muscle is plainly degenerating, possibly in association with the degeneration of the fibula, and it is notable that it is quite absent in many of the Pico-Passerine group (*Beddard*). In *Dacelo* it arises from the external corner of the tibial crest as a narrow tendon, instead of the more normal broad origin by muscle or fasciæ. It is joined by a few fibres from the tibia along the region of the fibula, and is inserted to the knee-capsule without the usual slip to the flexor of the middle digit. The same conditions exist in all the diastataxic forms and in some of the eutaxic forms. But in other eutaxic forms, notably *Ceryle americana* and *C. inda*, in the *Halcyones*, and *Ceyx*, it is still more reduced, being simply a long round tendon with the merest vestige of muscular fibres in it.

Peroneus profundus.—This muscle is relatively better developed, arising from the area of the tibia usually covered by the lower end of the fibula. This is the general condition, and suggests an increased strength in compensation

for the degeneration of the superficial muscle. The increase is notable in some of the eutaxic forms, e. g. *Ceryle americana* and *C. inda*.

Gastrocnemius.—In *Dacelo* (fig. 15, *tib.*, *mid.*, *ext.*) this muscle has the usual three heads, the middle head being the smallest and connected with the internal *adductor*. It is similar in the other Kingfishers, except that in *Halcyon rufa* all three divisions are reduced to tendon, perhaps an individual abnormality. I figure the muscle, as its arrangement in different Avian groups has considerable interest.

Fig. 15.



Leg-muscles of *Dacelo gigantea*.

fem., femur; *add.*, adductor; *semi-m.*, semi-membranosus; *ext.*, *mid.*, *tib.*, external, middle, and tibial heads of the gastrocnemius.

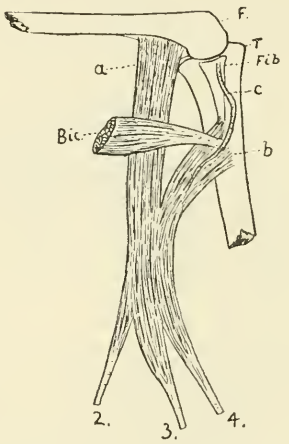
Plantaris.—This is small and normal in all.

Flexores perforantes et perforati of the second and third digits are similar in all, except that in *Ceyx* the muscle of the index is absent.

Flexores perforati of digits II., III., IV.—In *Dacelo* (fig. 16, p. 118) this muscle-complex arises by two heads, which join and give rise to the tendons for the digits. One head is fleshy and from between the condyles of the femur; the other also is fleshy and arises, rather unusually, from the fibula and

tibia near the insertion of the biceps. The *ambiens* muscle is completely absent, and there is no trace of an *ambiens* contributory to this muscle-complex. But there is present, in a reduced condition, a tendinous slip (fig. 16, *c*) from the head of the fibula, a slip which in many birds unites with the *ambiens* ligament before that passes into the muscle-complex. I describe and figure this muscle because, although it is similar in all the Kingfishers (except in *Ceyx*, where the

Fig. 16.



Leg-muscles of *Dacelo gigantea*.

F., femur; *T.*, tibia; *Fib.*, fibula; *Bic.*, cut edge of biceps; *a*, intercondylar head; *b*, tibial head of flexor perforatus; 2, 3, 4, tendons to digits II., III., IV.; *c*, ligament from head of fibula.

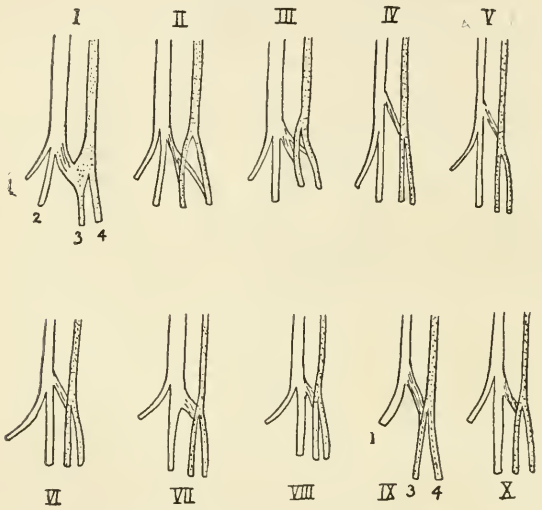
tendon to the index is absent), its varying conditions in different Avian groups still require examination. At present it seems to me probable that the head from the fibular region demands consideration in connection with certain rudiments which I described as *ambiens* rudiments (10), and that this, as well as the presence of the tendinous slip from the head of the fibula, tends to break down Garrod's sharp distinction between homalogonatous and anomalogonatous birds.

Flexor longus hallucis and *flexor profundus*.—The origin of these and their relation in the knee-capsule conform to the normal Avian type. The plantar tendons, however, show

specific peculiarities which I have figured, as much stress has been laid on these structures. In fig. 17 the tendons are all represented as arranged in the same position; the *flexor hallucis* is to the right and is dotted, the deep flexor is to the left and is not dotted, but that portion of it which represents the vinculum is marked with longitudinal lines. The hallux is to the left. Sundevall made one of the earliest contributions to knowledge of the interesting divergences in these tendons which occur among birds; but his attention was devoted specially to the Passerine foot, while Garrod (2) laid the foundation of a more general knowledge. According to his account, and subsequent research has strengthened his position, the normal Avian condition is that the *flexor hallucis* tendon crosses the *communis* tendon to be inserted to the hallux, but on its way sends a strong vinculum to the *communis*. In certain birds, however, he showed that the *hallucis* and *communis* tendons fused, and that from their conjoined mass slips were given off to the digits, the hallux slip arising markedly on the side of the *communis* tendon, not on the side of the *hallucis* tendon. He supposed the condition in *Momotus, Merops,* and *Dacelo,* where the *communis* obviously supplied the hallux, and where the *hallucis* tendon instead of supplying the hallux supplied other digits, to be a simple derivative of the foregoing stage. In a Kingfisher chick, the species of which was undetermined, I found the condition which Garrod thought intermediate between the most common arrangement and that in *Merops* and *Dacelo*. The *hallucis* and *communis* tendons fused, and from the common mass the tendons to the four digits arose, that of the hallux arising on the *communis* side. I think that there is much more to be said as to the primitive and derived conditions in birds generally, but for the present I may point out that, as the figures show, the typical Kingfisher condition, that most strikingly different from those more common in other birds, is for the so-called *hallucis* to supply digits 3 and 4, and for the so-called *communis* to supply the hallux and digit 2. This is extremely well seen in the eutaxic forms (fig. 17, p. 120, IV. to X.);

only a narrow vinculum connects the two tendons. In *Dacelo* (fig. 17, I.) and *Sauropatis*, and especially in the diastataxic as contrasted with the eutaxic *Ceryles* (fig. 17, II. and III.), the *communis* retains a more strong hold on the third and fourth digits by means of a branching vinculum,

Fig. 17.



Deep plantar tendons of Kingfishers.

I. *Dacelo gigantea.*
II. *Ceryle maxima.*
III. —— *alcyon.*
IV. —— *americana.*
V. —— *inda.*
VI. *Cittura.*
VII. *Halcyon pileata.*
VIII. —— *rufa.*
IX. *Ceyx rufidorsa.*
X. *Alcedo.*

In all the *communis* tendon (plain) is to the left, and the *hallucis* tendon (dotted) is to the right. The *vinculum* is striped. In all the tendon for the hallux is to the left (1), and the tendons for digits 2, 3, and 4 follow towards the right. (2) is missing in *Ceyx*.

so that in these Kingfishers the peculiarity is not so acutely marked.

Garrod made the interesting observation that when a vinculum is present it runs down from the *hallucis* to the *communis*, with the result that the hallux cannot be flexed without at the same time flexing the other digits by the pull

on the vinculum, whereas digits 2, 3, and 4 could be flexed independently of the hallux by contraction of the *communis* muscle. In the Kingfishers, where the hallux is supplied by the *communis*, a similar functional result is brought about in another way. The hallux cannot be flexed independently of the other digits by the action of the *communis*, as the vinculum from that runs down to the *hallucis* tendon; but digits 3 and 4 may be flexed, independently of the action of the hallux, by the *hallucis* muscle.

In this communication I do not propose to enter into the osteological modifications displayed in these Kingfishers, but I may mention that they also provide valuable evidence as to the relative specializations of eutaxic and diastataxic forms. I may now sum up in a few words. When the anatomy of Kingfishers is examined, it is found that the differences present may, in a number of cases, be regarded as showing a greater or less degree of specialization. The group is to be regarded as marching in a definite direction, many of the organs tending towards definite changes which may be summed up as specialization. There is no *rigid* correlation between the degrees of specialization of different organs in the same species; in some species certain changes shoot out beyond others, but there is a general correlation, so that if any species be far advanced in one organ it is more likely to be far advanced in other organs, or to have a higher average of advance among all its organs, it being remembered that advance in such anatomical arguments means change from common, ancestral, or generalized type, whether such change be evolution or involution. The change from diastataxy to eutaxy is one of these advances or specializations, and in the Kingfishers, as in the Columbidæ, it is associated with a high average of advances in other organs. I am not here concerned with what may be called the motive force of specialization. It is plain that the mode of its occurrence offers a specious argument to those who would see in evolution evidence of a directive impulse, resident in organisms, and the active agent in their

phylogenetic modification. But it will be more in accordance with scientific reserve if we interpret the kind of facts set out in this paper as evidence that the direction of variation is one of the characters that define organic groups. It is obvious that this character is not likely to be exempt from the phylogenetic strengthening, of which we have evidence in the case of other characters.

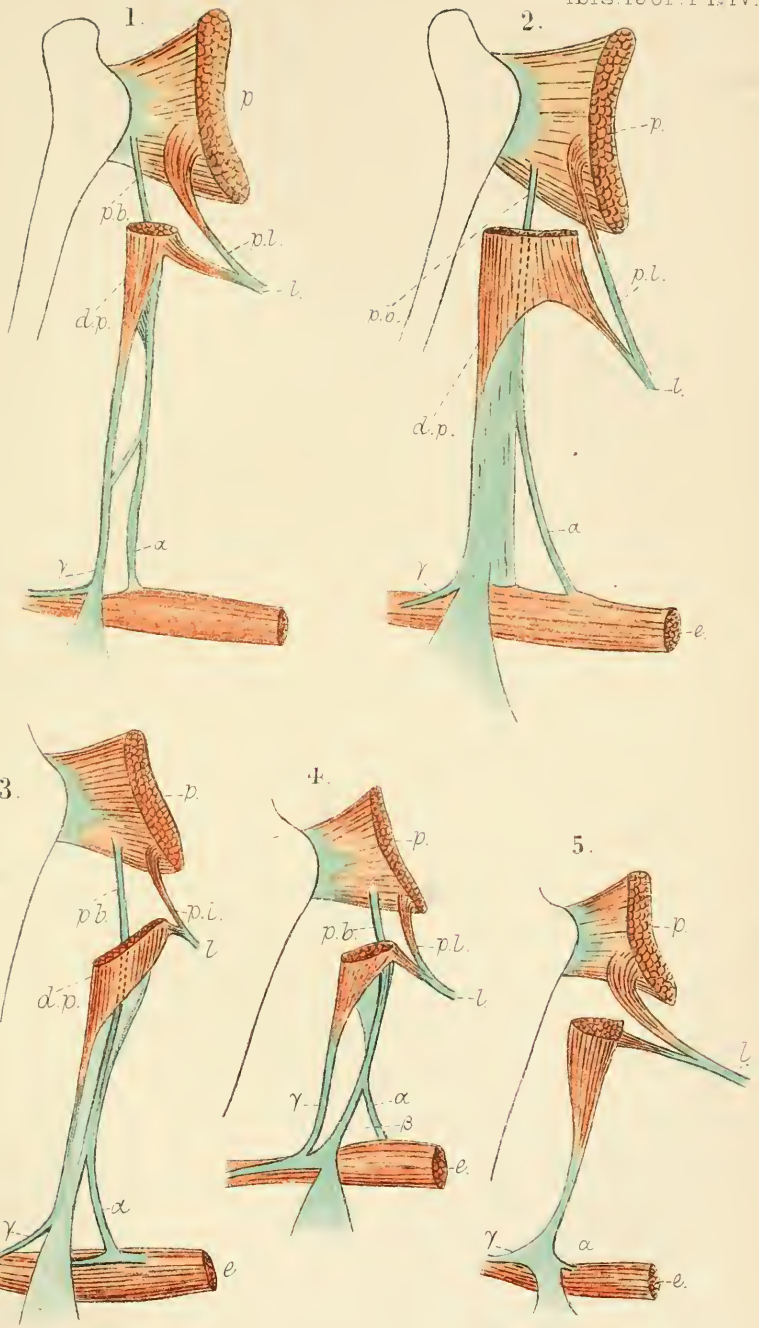
List of papers referred to.

(1) Wray.—"On some Points in the Morphology of the Wing of Birds." P. Z. S. 1887, p. 343.
(2) Garrod.—"On the Disposition of the Deep Plantar Tendons in different Birds." P. Z. S. 1875, p. 339.
(3) Cunningham, R. O.—"Notes on some Points in the Anatomy of three Kingfishers." P. Z. S. 1870, p. 280.
(4) Beddard.—"On some Points in the Anatomy of the Kingfishers." P. Z. S. 1896, p. 603.
(5) Fürbringer.—Untersuchungen zur Morphologie und Systematik der Vögel. 1888.
(6) Beddard.—The Structure and Classification of Birds. 1898.
(7) Chalmers Mitchell.—"Quintocubitalism in the Wing of Birds." J. Linn. Soc., Zool. vol. xxvii. p. 210.
(8) Pycraft.—"Aquintocubitalism in the Wing of Birds." J. Linn. Soc., Zool. vol. xxvii. p. 237.
(9) Gadow.—"Aves" in Bronn's Thier-Reich.
(10) Chalmers Mitchell.—"On the Perforated Flexor Muscles in some Birds." P. Z. S. 1894, p. 495.

EXPLANATION OF PLATES IV. & V.

Fig. 1. Alar muscles and tendons of *Dacelo gigantea.*
2. „ „ *Ceryle maxima.*
3. „ „ *C. alcyon.*
4. „ „ *Sauropatis chloris.*
5. „ „ *Ceryle americana.*
6. „ „ *C. inda.*
7. „ „ *Cittura cyanotis.*
8. „ „ *Halcyon pileata.*
9. „ „ *H. rufa.*
10. „ „ *Alcedo asiatica.*

All the figures represent the alar muscles and tendons. The outline of the humerus is to the left. Tendons and fasciæ are coloured blue; muscles red.



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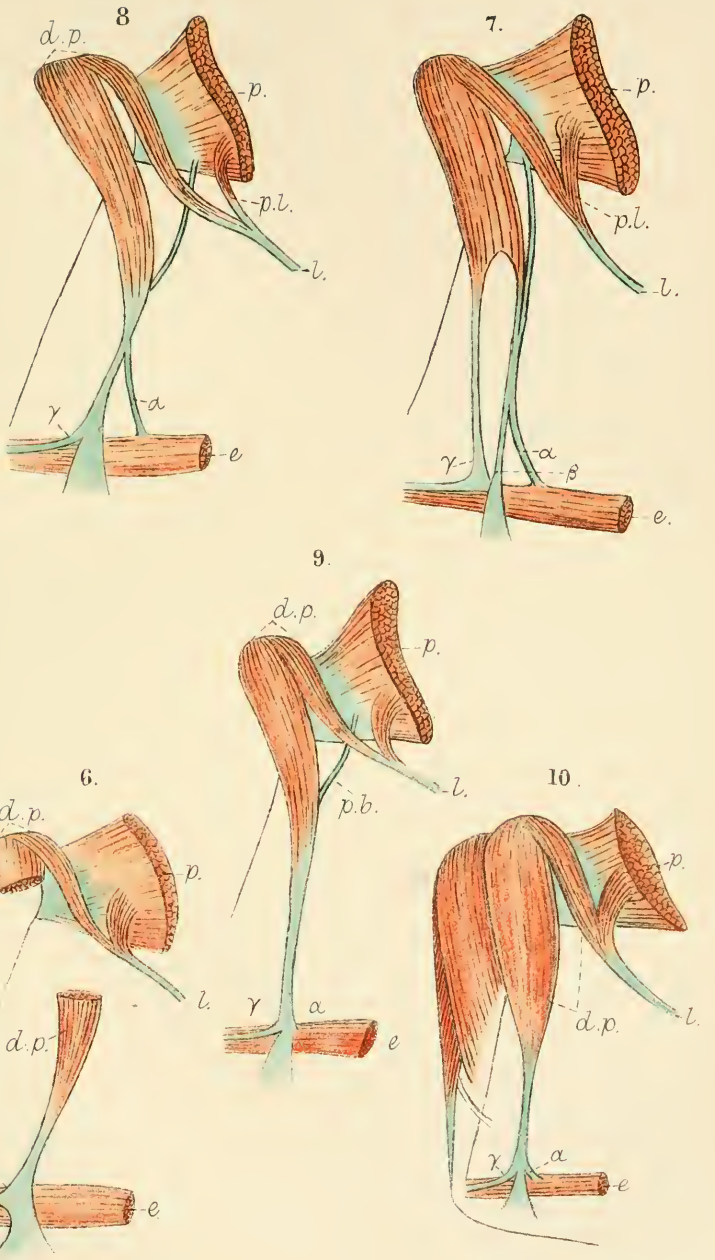
ALAR MUSCLES OF KINGFISHERS.



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ALAR MUSCLES OF KINGFISHERS.

p., pectoralis major.
p.l., „ longus slip.
p.b., „ brevis slip.
d.p., deltoides patagialis.
e., extensor metacarpi radialis.
α, *β*, *γ* { Subdivisions of the *brevis* tendon, named by Fürbringer: *γ* is always most near the humerus, *i. e.* to the left in the figures; *α* most near the wrist, *i. e.* to the right in the figures; *β* is median, and usually forms a fan-shaped expansion.

IX.—*Report on the Anniversary Meeting of the Deutsche ornithologische Gesellschaft.* By E. Hartert (Delegate of the B.O.U.).

Those members of our Union who have ever fallen into the hands of the German Ornithological Society during one of their annual gatherings will easily believe me if I say that I was excellently received and with all the honour due to the delegate of the B.O.U., when I arrived in Leipzig on October 5th, 1900, to represent the sister Union at the fiftieth anniversary of the German Society. In fact, it was looked upon as a special compliment from our Union that I was selected as the representative, connected, as I am, so closely with the German Society, and so intimate as I have long been with many of its members.

With the exception of Dr. Otto Herman, of Budapesth, I was the only foreign delegate, but many German Scientific Societies had sent representatives to Leipzig.

Professor Rudolf Blasius, as President of the Society, opened the Meeting officially on October 6th.

Herr Hermann Schalow gave an interesting *résumé* of the history of the Society, which consists, in fact, of two former societies, amalgamated since 1875. The older of these had existed since 1845, but at first only as a section of the annual "Naturforscher-Versammlungen." In 1850, however, it was separated as an independent society. Only one of the original founders is still alive, Herr Kunz of Leipzig, who was present on this occasion, and was as active as a man in his best years.